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1  
2  
3 24 **Abstract**  
4

5 25 Sexual selection favours the expression of traits in one sex that attract members of the opposite sex  
6  
7 26 for mating. The nature of sexually selected traits such as vocalisation, colour and ornamentation,  
8  
9 27 their fitness benefits as well as their costs have received ample attention in field and laboratory  
10  
11 28 studies. However, sexually selected traits may not always be expressed: colouration and ornaments  
12  
13 29 often follow a seasonal pattern and behaviours may be displayed only at specific times of day.  
14  
15 30 Despite the widely recognised differences in the daily and seasonal timing of traits and their  
16  
17 31 consequences for reproductive success, the actions of sexual selection on the temporal organisation  
18  
19 32 of traits has received only scant attention. Drawing on selected examples from bird and mammal  
20  
21 33 studies, here we summarise the current evidence for sexual selection on seasonal and daily timing.  
22  
23 34 We highlight that molecular advances in chronobiology have opened exciting new opportunities for  
24  
25 35 identifying the genetic targets that sexual selection may act on to shape the timing of trait  
26  
27 36 expression. Furthermore, known genetic links between daily and seasonal timing mechanisms lead  
28  
29 37 to the hypothesis that selection on one time scale may simultaneously affect the other as well. We  
30  
31 38 emphasize that studies on the timing of sexual displays of both males and females from wild  
32  
33 39 populations will be invaluable for understanding the nature of sexual selection and its potential to  
34  
35 40 act on differences within and between the sexes in timing. Molecular approaches will be important  
36  
37 41 for pinpointing genetic components of biological rhythms that are targeted by sexual selection, and  
38  
39 42 to clarify whether these represent core or peripheral components of endogenous clocks. Finally, we  
40  
41 43 call for a renewed integration of the fields of evolution, behavioural ecology and chronobiology to  
42  
43 44 tackle the exciting question of how sexual selection contributes to the evolution of biological clocks.  
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45 46

46 45 **Keywords:**  
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49 46 Sexual selection, circadian rhythm, circannual rhythm, timing of reproduction, display behaviour  
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## 48 Introduction

49 Sexual selection occurs when individuals of either sex experience enhanced mating success based on  
50 their display of behaviours or ornaments [1]. With sexual selection defined as selection on traits that  
51 improve reproductive success [2], precise timing of ornaments and behaviour becomes a key  
52 element as well. While much work has been devoted to study *how* sexual selection leads to sexual  
53 dimorphism in morphological or behavioural traits (i.e., big weapons, colourful ornaments, complex  
54 behaviour), less attention has been paid to physiological traits that determine *when* a trait will be  
55 expressed, even though variation in the timing of trait expression can also result in sexual selection.

56  
57 After briefly summarizing the concepts in sexual selection that pertain to this framework, we follow  
58 with a short review of the role of the neurobiological and molecular regulation of circadian rhythms  
59 as well as its involvement in annual timing. Understanding the relationship between circadian and  
60 circannual mechanisms may provide insight into the pathways that potentially affect variation in  
61 timing simultaneously on both daily and seasonal scales. We then present selected studies especially  
62 from well-known avian taxa but also from mammal species as evidence for daily and annual timing  
63 of displays as potential sexually selected traits. As examples of traits in the daily and annual time  
64 scale domains we present the timing of dawn chorus, of reproductive readiness and of arrival at  
65 breeding grounds for birds, and timing of hibernation termination and of daily activity times for  
66 squirrels (*Sciuridae*), one of the few mammalian taxa for which suitable data are available.  
67 Throughout this review, we aim to identify areas of future study to bolster evidence of timing being  
68 a sexually selected trait.

69

## 70 *Sexual selection and its application to timing processes*

71 From its first formulation [3], sexual selection theory has been invoked to explain the existence of  
72 certain morphological or behavioural traits (secondary sexual characters) that can increase the  
73 mating success of an individual. In this review, we define sexual selection as among-individual

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3 74 variation in reproductive success and consider it to be one of three components that together  
4  
5 75 constitute natural selection; the other two components being fecundity (fertility) and viability  
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7 76 (survival) selection [4]. Sexual selection is a powerful evolutionary force based on social interactions,  
8  
9 77 and fostered by the existence of between-sex differences in mating potential and reproductive  
10  
11 78 investment [5]. In the majority of species, it is the male that displays his quality, to attract mates  
12  
13 79 (inter-sexual selection) or to compete with rivals in agonistic encounters (intra-sexual selection),  
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15  
16 80 although the opposite pattern or mutual sexual selection also frequently occurs [1]. At an intra-  
17  
18 81 specific level, the outcome of fights and choices depends on the expression of secondary sexual  
19  
20 82 traits that can vary greatly among individuals. This variability represents the substrate for sexual  
21  
22 83 selection [6–8]. The expression of secondary sexual traits in general is considered costly because  
23  
24 84 these traits usually do not increase survival; instead, they require crucial resources to be converted  
25  
26 85 into mating potential and reproductive success [9]. In this view, there exists a trade-off between the  
27  
28 86 benefits of sexual selection and the costs paid through natural selection [10].  
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32 87 Throughout this review, we consider traits to be potentially under sexual selection if they increase  
33  
34 88 the number of successful matings for an individual, thereby enhancing its reproductive success [2].  
35  
36 89 We focus primarily on traits that boost mate attraction (inter-sexual selection), but also consider  
37  
38 90 competitive ability (intra-sexual selection) – if it increases mating success – to play a role. Applied to  
39  
40 91 the timing of daily or seasonal events, we expect that traits may be under sexual selection if they  
41  
42 92 determine mating success (or proxies like number of mating partners), exhibit variation among  
43  
44 93 members of one sex in timing, and impose costs on their bearer. One prominent example is the  
45  
46 94 dawn song of male songbirds (detailed below). If there exists variation among males in daily or  
47  
48 95 seasonal singing times, males that sing earlier in the day or season obtain more fertilisations and  
49  
50 96 early singing is more costly than late singing, sexual selection likely is at play. This contrasts with  
51  
52 97 timing of traits that are well-known to be under natural (fecundity or viability) selection, like the egg  
53  
54 98 laying dates of many songbirds or parturition times in mammals [11–18]. Here, ecological selection  
55  
56 99 pressures like food availability or predation risk determine the number of offspring produced.  
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3 100 The assumption of costs for sexually selected traits also postulates the existence of interactions  
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5 101 between sexual and fecundity/viability selection on the timing and the quality (e.g., size, colour,  
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7 102 complexity) of a trait (Fig. 1). Staying with the example of song in male birds, sexual selection would  
8  
9 103 be expected to favour an early expression of this trait because it would increase mating success  
10  
11 104 while viability selection may act against the display of early song, perhaps because singing too early  
12  
13 105 in the day or in the season is energetically costly or increases predation risk [19–21]. Likewise, a high  
14  
15 106 quality of trait expression (for example long song bouts or complex song) would be favoured by  
16  
17 107 sexual selection while fecundity/viability selection may reject the expression of the highest quality  
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19 108 traits, perhaps because of associated costs. In this view, only individuals of the highest quality would  
20  
21 109 be able to afford the costs of displaying song early and at high quality, and would gain maximal  
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23 110 reproductive success [22] (Fig. 1). However, the interactions between trait timing and trait quality  
24  
25 111 may not simply be additive but could be more complex. One reason for this complexity could be that  
26  
27 112 trait quality primarily follows a Bateman’s gradient (higher trait quality results in more matings,  
28  
29 113 leading to higher reproductive success), while variation in trait timing can additionally result in  
30  
31 114 variations in the operational sex ratio (for example, males with an early trait expression face fewer  
32  
33 115 competitors and more potential mates) [2]. As a result, males that display a trait early may gain  
34  
35 116 substantial mating success even if the quality of the trait they display is suboptimal, and males that  
36  
37 117 display late may only be successful if their traits are of sufficient quality. It will be a rewarding  
38  
39 118 challenge for future research to provide both a firm theoretical basis and empirical tests of such  
40  
41 119 interactions. It should be noted that future work should incorporate both sexes equally in theoretical  
42  
43 120 considerations, as there appears to exist a sex-bias not only in empirical (see below), but also in  
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45 121 theoretical work (e.g., [23,24].  
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53 123 **Common molecular mechanisms of daily and seasonal timing as a substrate for sexual selection**  
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55 124 Neural and neuroendocrine regulation of daily and seasonal timekeeping depends on  
56  
57 125 photoneuroendocrine systems (PNES) with many conserved features in birds and mammals. Detailed  
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126 reviews of the molecular and neuroanatomical features of the PNES, and a comparison of  
 127 differences among vertebrate groups can be found elsewhere (e.g., [25]). Our brief overview  
 128 primarily seeks to inform consideration of the likely genetic substrates for sexually selected  
 129 timekeeping by outlining major components and genes involved in daily and seasonal clocks. An  
 130 existing bias towards molecular studies on vertebrates being conducted on laboratory mammals  
 131 (particularly rodent species) is reflected in this section.

132 Broadly conserved features of the PNES include opsin-based light sensing pathways for daily and  
 133 seasonal entrainment of clocks, circadian rhythm generation through transcriptional – translational  
 134 feedback loop mechanisms running in hypothalamic pacemakers, and a key role for the pars  
 135 tuberalis and hypothalamic tanycytes in seasonal neuroendocrine regulation. Important differences  
 136 include varying complements of specific circadian clock genes (e.g. *per1* in mammals not birds), and  
 137 differing emphasis on melatonin for circadian organisation in birds as opposed to seasonal  
 138 photoperiodic organisation in mammals.

139 In birds, photic information reaches circadian timing systems through photoreceptors in the pineal  
 140 gland and various opsin-expressing brain areas, with the eyes playing a species-specific role in  
 141 circadian organisation (that perhaps is more to do with melatonin secretion than actual  
 142 photoreception) [26–30]. Avian photoperiodic control of seasonal reproduction involves primarily  
 143 deep encephalic photoreceptors [29,31,32]. In both birds and mammals the suprachiasmatic nucleus  
 144 (SCN) contains a molecular circadian oscillator (Fig.2C), which is entrained by light information and  
 145 regulates nocturnal melatonin release by the pineal gland. The avian pineal gland also contains a  
 146 self-sustained circadian oscillator that is intrinsically light sensitive [33], which is not the case in  
 147 mammals. In birds, the SCN, the eyes, and the pineal jointly perform circadian pacemaker functions,  
 148 regulating daily timing in physiology and behaviour (Fig.2A; [30]). In contrast, in mammals the SCN is  
 149 the dominant circadian pacemaker (Fig.2B) and photoperiod is exclusively sensed through the eye,  
 150 where photoreceptors (notably containing melanopsin, OPN4) project to the SCN (Fig.2B)[34].

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3 151 Within circadian pacemaker structures, as well as in target tissues, circadian rhythms at the cellular  
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5 152 level are maintained by molecular oscillations in so-called transcription translation feedback loops  
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7 153 (TTFLs) [28]. In essence, TTFLs depend on transcriptional activators (e.g. CLOCK, BMAL1), which drive  
8  
9 154 the expression of transcriptional repressors (e.g. CRYPTOCHROME, PERIOD), which generate  
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11 155 negative feedback onto the activators. Entrainment of these feedback loops depends on light-  
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13 156 dependent effects on the expression of negative elements, mediated through phosphorylation-  
14  
15 157 dependent transcription factors such as CREB [35]. The dynamics of TTFLs depend heavily on post-  
16  
17 158 translational effects such as phosphorylation and ubiquitination, which affect subcellular localisation  
18  
19 159 and stability of the core transcriptional regulators. The actions of these core transcriptional  
20  
21 160 regulators on so-called “clock controlled genes” (including further transcription factors such as Tef,  
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23 161 Hlf and Dbp, see Fig. 2) are responsible for overt circadian rhythms in cellular physiology (see  
24  
25 162 [www.genecards.org](http://www.genecards.org) for all abbreviations).

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29 163 In both birds and mammals, the circadian timing system is also essential for measuring changes in  
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31 164 day-length, which then trigger seasonal neuroendocrine responses and synchronise circannual  
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33 165 rhythms [29,36]. Especially in mammals, melatonin provides an important signal for the duration of  
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35 166 darkness (and thus daylength), forming a critical regulating input to the pars tuberalis (PT) of the  
36  
37 167 pituitary stalk, a crucial structure for circannual timing (Fig. 2CD). The PT produces thyroid-  
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39 168 stimulating hormone (TSH) under long summer days, through a mechanism thought to depend in  
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41 169 mammals on melatonin-dependent control of TTFL oscillations and their impact on the expression of  
42  
43 170 the clock-dependent transcriptional co-activator Eya3. PT Eya3 expression peaks some 12 h after  
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45 171 dusk and appears to be directly suppressed by melatonin. This forms a “coincidence timer”  
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47 172 mechanism ensuring that Eya3 levels only rise when night length falls below a critical duration in  
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49 173 spring [27]. Eya3 also enhances its own induction, thereby leading to positive feedback and full  
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51 174 induction within a few days of long photoperiod [37]. In birds, photoperiodic control of PT  
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53 175 production of TSH is also critical for the photoperiodic control of reproduction, and is also associated  
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55 176 with strong Eya3 induction [38,39]. Here, however melatonin does not relay the photoperiodic  
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177 message, but instead photoreceptive, cerebro-spinal fluid (CSF)-touching neurons containing OPN5,  
 178 neuropsin, or VAopsin project to the PT (Figs. 2A and 2D are illustrating this in mammals; [32,40–  
 179 42]). Details of the activation pathway leading to TSH induction, including the putative role of Eya3  
 180 therein, remain to be established.

181 Downstream of TSH, induction of type II iodothyronine deiodinase (DIO2) expression in tanycytes  
 182 lining the 3<sup>rd</sup> ventricle wall is a conserved response to long photoperiod in birds and mammals. DIO2  
 183 converts thyroxine (T4) to the active form of thyroid hormone, triiodothyronine (T3). In long day  
 184 breeders, T3 stimulates the release of gonadotropins (*i.e.*, follicle stimulating hormone and  
 185 luteinizing hormone) by the pituitary gland through interaction with hypothalamic gonadotropin  
 186 releasing hormone (GnRH) producing neurons, resulting in gonadal development (for review see  
 187 [43]).

188 Overall, the selected regulatory networks summarised in this section offer a range of possible  
 189 candidates through which sexual selection on daily or seasonal timing characteristics might operate.  
 190 After all, selection requires heritable phenotypic variation (*i.e.*, variation based on genetic  
 191 mechanisms) to generate evolutionary change. Below we will discuss which components of these  
 192 networks (central versus peripheral) may more likely be targets of sexual selection. We will also  
 193 provide examples for specific clock genes/networks that are known or suspected to be involved in  
 194 the timing of potentially sexually selected traits in the subsequent sections that discuss specific  
 195 studies. It is also important to emphasize that other (non-PNES) physiological processes like  
 196 endocrine signals are potent modifiers of daily and seasonal time-keeping, representing potential  
 197 additional pathways and targets of selection (detailed further in the section below, see also [44]).  
 198 For example, it has been shown in both mammals and birds that sex steroids (androgens, estrogens)  
 199 can affect circadian functioning, although phenotypic effects are species-specific. These sex steroids  
 200 can cause both permanent (organisational) or temporary (activational) sex differences in daily timing  
 201 [44,45]. Mechanistically, the actions of sex steroids are accomplished by binding to receptors that

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3 202 are located in the SCN itself, but also in pathways that provide input to and receive information from  
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5 203 the SCN (at least in mammals, less is known in birds) [45].  
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#### 10 205 **Which PNES (or non-PNES) components may be under sexual selection?**

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12 206 When discussing potential effects of sexual selection on the functioning of biological clocks, one may  
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14 207 also consider the clock components that may be targeted. Specifically, the question arises whether  
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16 208 one would expect sexual selection to act on central or peripheral clock components (see also [44]).  
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18 209 Selection on parts of the central clock (on core clock genes/networks and their expression in  
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20 210 pacemaker structures, see molecular section above) may consequently permeate all clock tissues  
21  
22 211 and exert pleiotropic effects on various traits – possibly at all times. Hence, selection on core clock  
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24 212 components may be expected to lead to general (permanent, organisational) differences between  
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26 213 the sexes, like for example a male-specific expression of certain traits like antlers, plumage  
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28 214 ornaments, courtship displays or a female-specific expression of traits such as mate choice  
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30 215 behaviour, cryptic colouration, or maternal behaviour in uniparental species. Such pervasive sex  
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32 216 differences may be more likely generated (or exaggerated) by the actions of fecundity (e.g., ability to  
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34 217 perform courtship, establish a territory, produce offspring) or viability (e.g., avoid predation)  
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36 218 selection, i.e., by the other two components of natural selection. However, the strength of any  
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38 219 pleiotropic effects of central clock components will depend on the nature of their connections with  
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40 220 other clock (or non-clock) components (for a related discussion concerning reproductive physiology  
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42 221 (see [46,47])). For instance, in mammals the SCN plays a far more dominant role in both daily and  
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44 222 seasonal processes than in birds (see molecular section above, Fig. 1), and thus selection on  
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46 223 processes that affect the functioning of the SCN may have a larger impact on circadian phenotypes  
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48 224 in mammals compared to birds.  
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55 226 By contrast, *sexual* selection would be expected to act on between-individual variation in one sex in  
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57 227 the timing of signal expression (see sexual selection section above), which may be more likely  
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generated by clock controlled genes (ccg's, see molecular section above) that mediate the clock output and/or modulate of gene functioning, perhaps even in a tissue-specific manner [48]. The latter may also involve tissue-specific DNA methylation [49], which can have sex-specific phenotypic effects (see below). Also, other systems like endocrine signals may be important (see also molecular section above), especially when the display of traits only happens at specific times of year, like the dawn song of birds that is displayed during the reproductive season only ([44,50], see also bird examples below).

### **Indirect selection on timing mechanisms**

To date, relatively little research has focused on the impact of sexual selection for timing on the functioning of the PNES, but there exist ample examples for the actions of fecundity/viability or artificial selection on PNES components (reviewed in [51–54]), of which a few select ones are summarized below. Here we argue that a retrospective analysis of the genetic bases of “domestication selection” in laboratory rodents and in commercial poultry breeds may be informative. In laboratory rodents, the regulation of reproduction by seasonal changes in daylength via the PNES has been selected against, presumably because a weakened or non-functional PNES favours higher reproductive rates in colonies held on ambiguous LD 12:12 regimes, standard in rodent facilities [55,56]. For example, the mouse strain C57BL/6J is severely compromised in its ability to produce melatonin, essential for suppressing reproduction in short days. The melatonin deficiency in pineal glands of C57BL/6J mice arises from mutations in melatonin-producing enzymes (HIOMT and AANAT), likely an inadvertent by-product of selection for breeding under laboratory conditions [57,58]. In layer breeds of poultry [59], domestication has had a strong selective effect on the TSH receptor gene [55,56], with domesticated species carrying a mutant allele that may be responsible for a reduced seasonality and consequently a greater readiness to breed under short days.

253 The existence of substantial within- and between-species differences in PNES mechanisms likely  
 254 reflects the actions of fecundity or viability selection. A prominent example is the timing of  
 255 reproduction in *Peromyscus* mice, which show considerable latitudinal variation within and between  
 256 species of this genus in breeding times and responsiveness to short photoperiod [53,60]. Artificial  
 257 directional selection experiments yielding lines of wild-derived *Peromyscus* mice with either strong  
 258 or no responsiveness to short photoperiod (in inhibiting reproductive readiness [61]) support the  
 259 hypothesis that fecundity or viability selection has shaped variation in the PNES. These selection-line  
 260 *Peromyscus* mice showed clear differences in iodomelatonin binding in certain brain areas and in the  
 261 number and location of GnRH neurons [62,63]. Furthermore, selection lines differed in the period of  
 262 their free-running circadian rhythms ( $\tau$ ), although that appeared to be unrelated to their  
 263 photoperiodic responses [64]. Fecundity or viability selection may also have affected the timing of  
 264 expression of PNES genes in wild populations of a common Eurasian song bird, the great tit (*Parus*  
 265 *major*). In a common garden experiment, great tit males from a Swedish (latitude 57°N) and a  
 266 German (47°N) population differed in the timing of mRNA expression of Per2, DIO2, DIO3, GnRH and  
 267 FSH- $\beta$  following exposure to a single long day, which simulated an abrupt change from short to long  
 268 days [65]. These differences in the timing of gene expression may be a result of adaptations to  
 269 breeding at different latitudes, as Swedish great tits initiate reproduction a few weeks later and thus  
 270 at longer daylengths than German birds [66].

271 Laboratory studies have also documented links between circadian clocks and reproductive-related  
 272 behaviour, specifically between the speed of the circadian clock and behavioural traits and *vice*  
 273 *versa*. For instance, experimental selection in mice for nest building behaviour resulted in individuals  
 274 that build bigger nests having a shorter circadian period length than individuals with hardly any nest  
 275 building [67]. Likewise, selection in mice for aggression also yielded a circadian phenotype with  
 276 shorter circadian periods for aggressive mice [68]. In humans, circadian chronotype has been linked  
 277 to personality traits and even life history strategies [69]. In this study, individuals self-characterised  
 278 as morning-types (or 'larks') showed evidence for following a 'slow' life history in psychological and

behavioural traits while evening-types ('owls') were more likely to follow a 'fast' life history with opposing trait combinations. Because the circadian system is mechanistically tightly coupled to annual timing (see molecular section above), differences in daily timing may also be linked to differences in annual timing. Daily timing of display behaviour may thus convey information about the annual timing of the signaller. Indeed, a few phenotypic connections between circadian and annual timing systems have recently been discovered. For example, a phenotypic link between daily (first morning departure from the nest) and seasonal chronotypes (nest initiation dates) has recently been documented in females of two songbird species [70]. Additional specific examples will be discussed below.

## **Timing as a sexually selected trait in birds**

### Daily timing

In several species of socially monogamous songbirds, the pre-dawn period is a critical time for mating with partners outside of the social pair [71–75]. Much of the activity during this period before dawn is spent singing, participating in what is known as the dawn chorus [76,77]. The variation in the time at which an individual starts singing during this pre-dawn period correlates with variation in extra-pair paternity; for example, male blue tits (*Cyanistes caeruleus*) which join the dawn chorus first are the most successful within the population at gaining extra-pair paternity [72,74,76]. Thus, the timing of dawn song affects male mating success, and therefore appears to be a sexually selected signal.

Recent studies suggest that components of circadian clocks may determine the timing of male activity onset, and thereby their initiation of dawn song and subsequent mating success. Experimental disruption of the circadian rhythm of circulating melatonin levels delayed the onset of daily activity in wild male great tits compared to sham-treated individuals. Importantly, individuals with an experimentally delayed activity onset were more likely to be cuckolded (i.e., had a larger

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3 304 proportion of extra-pair nestlings in their nest), thus decreasing their genetic reproductive success  
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5 305 (Fig.2) [78]. These data suggest that females prefer to copulate with males that become active  
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7 306 earlier in the day. This interpretation is corroborated by an earlier study on great tits brought into  
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9 307 captivity as nestlings. When the free-running period length ( $\tau$ ) of their activity rhythms was recorded  
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11 308 under constant dim light, individuals sired by an extra-pair father displayed a shorter  $\tau$  than siblings  
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13 309 sired by their social father [79]. This same study showed a relatively high heritability of circadian  
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15 310 rhythms, suggesting that females may prefer to engage in extra-pair copulations with males that  
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17 311 have a fast circadian rhythm.

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21 312 Taken together, these studies in songbirds indicate that sexual selection likely is an important  
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23 313 selective force that shapes circadian phenotypes. However, many questions still remain open. For  
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25 314 example, while evidence is accumulating that dawn song is aimed at attracting mates (i.e. inter-  
26  
27 315 sexual selection), it could also function in male-male competition, implying a different kind of  
28  
29 316 selection (i.e. intra-sexual selection, [72,75,80,81]). This distinction has implications for the receiver,  
30  
31 317 because in inter-sexual selection it would be females that choose males based on their circadian  
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33 318 phenotype, while in intra-sexual selection the choosy sex would be other males. Both types of sexual  
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35 319 selection require that early song signals an aspect of male quality that the receiver recognises, but  
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37 320 what aspect of quality is conveyed is presently unclear. Even more interesting, both types of  
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39 321 selection require that the receiver is able to perceive the signal, i.e. is up and about equally early.  
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41 322 Hence one critical prediction is that (certain) females and/or males also become active early during  
42  
43 323 the period of the dawn chorus. However, there exists a researcher sex-bias and the timing of the  
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45 324 behaviour of females is much less understood [82]. Results from the few studies that have been  
46  
47 325 conducted on female blue and great tits thus far are puzzling. Females of both species do advance  
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49 326 their activity onset and are active earlier on days that immediately precede the start of egg laying –  
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51 327 but in general they tend to get up later than males [83,84]. Moreover, natural or manipulated  
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53 328 female activity onset times do not correlate with extra-pair young in her brood [84]. Thus, how early  
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55 329 male song may be selected for is still unclear. Interestingly, when female great tits were given a  
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3 330 melatonin implant that was identical to the one that delayed the onset of activity in males [78], it did  
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5 331 nothing to their daily activity onset but delayed their seasonal reproductive timing (clutch initiation  
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7 332 dates [85]).  
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10 333 From the experimental evidence presented above, it is tempting to speculate that the circadian  
11  
12 334 hormone melatonin is involved in mediating individual variation in activity onset and thus  
13  
14 335 participation in the dawn chorus in male birds. The melatonin-induced delay in the onset of activity  
15  
16 336 in male great tits described above may result from the implants swamping diel rhythms in  
17  
18 337 endogenous melatonin, thus weakening circadian rhythms and altering chronotype, i.e. the time  
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20 338 when individuals become active in the morning with respect to sunrise [78]. Such effects of  
21  
22 339 continuous-release melatonin implants on the chronotype of entrained as well as periods of free-  
23  
24 340 running circadian rhythms have indeed been demonstrated in songbirds [86–89]. Furthermore, it has  
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26 341 recently been shown that zebra finches (*Taeniopygia guttata*) decrease nocturnally elevated  
27  
28 342 melatonin levels roughly 2 hours before lights on, with actual times of melatonin decreases differing  
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30 343 among individuals [90]. It is therefore possible that natural variation exists among males in the  
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32 344 timing of their early-morning melatonin decline, which in turn may influence their activity onset.  
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34 345 Additionally, there could be interactions between the circadian system and sex steroids like  
35  
36 346 testosterone, which is secreted at elevated levels at the start of the mating season and which may  
37  
38 347 contribute to this variation in early morning melatonin-decrease and/or activity onset. Testosterone  
39  
40 348 can affect circadian properties in some avian species, leading to changes in  $\tau$ , chronotypes and  
41  
42 349 entrainment properties (see also discussion in [44,91]). However, the onset of the pre-dawn crowing  
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44 350 in roosters, which is under circadian control, is not influenced by testosterone administration [92].  
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50 351 Moreover, one critical link is still not fully established, which concerns the link between  $\tau$  measured  
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52 352 under constant conditions in the lab and the chronotype in nature. While studies in captivity on birds  
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54 353 and humans convincingly show that a short period length is related to an onset of activity before  
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56 354 lights-on [93,94], in captive great tits  $\tau$  of individuals was not correlated with their chronotype [79].  
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Overall, we still have little information on the relationship between endogenous and overt rhythms in wild species. A recent study on Eurasian blackbirds (*Turdus merula*) has attempted to fill this gap [95]. Using automated radio telemetry, daily activity rhythms of urban and forest blackbirds were first recorded in the field, where urban birds showed a much earlier onset of dawn activity than the forest conspecifics. Blackbirds were then caught and their endogenous period length assessed in constant dim light in the laboratory. Urban blackbirds showed a shorter period length than the forest birds, and this correlated at the individual level with an earlier onset of activity in the field. Conversely, forest birds showed high variation in period length in the laboratory, but little or no variation in timing in the field, as they all precisely synchronised to dawn. As early dawn timing has been associated with higher extra-pair paternity gain in songbirds [72,74], an intriguing possibility is that urban life might select for early chronotypes and faster clocks. Again, altered daily patterns of melatonin may play a mechanistic role here. Indeed, when the same blackbirds were exposed to realistic levels of artificial light at night in captivity, simulating urban-like conditions, nocturnal melatonin levels dropped significantly, and especially in the early morning [96]. Such a drop was related at the individual level to the amount of activity that a bird showed in the morning, regardless of the origin of the animal (urban vs. forest). This suggests that light at night, via changes in melatonin levels, can promote the emergence of early chronotypes, which could be favoured in urban environments [74,97]. This hypothesis requires further testing, but the availability of novel molecular tools might inspire further studies [98]. Indeed, it is now possible to infer the endogenous rhythm period of an animal using skin biopsies rather than having to maintain animals in captivity [99]. This could facilitate the collection of novel data to link chronotype and period length in natural populations.

Establishing a link between natural chronotype and  $\tau$  in wild animals remains important because the circadian free-running period is not expressed under natural conditions and therefore cannot directly be subjected to sexual (nor fecundity/viability) selection. Circadian phase of entrainment (chronotype) is likely the phenotype that is selected for, but selection may also act on behavioural



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3 381 traits that may correlate with chronotype or other aspects of the circadian phenotype (see section  
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5 382 ‘Indirect selection on timing mechanisms’).  
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11 384 Annual timing as a sexually selected trait in birds  
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13 385 Many species of birds breed on a seasonal basis after which they regress their reproductive system  
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15 386 and enter a non-breeding state [100]. Being able to breed requires a re-activation of the regressed  
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17 387 reproductive system many weeks in advance of actual egg laying [100], and individuals that begin  
18  
19 388 reproductive development later or more slowly than conspecifics will also display reproductive  
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21 389 behaviours later and can be outcompeted by early individuals and/or selected against by potential  
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23 390 mates [101,102], but see [103]. Sexual selection on the timing of reproductive development likely is  
24  
25 391 stronger for males than for females [104], and may lead to earlier gonadal recrudescence in males  
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27 392 compared to females [105,106]. This differential timing results from male reproductive success being  
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29 393 strongly influenced by his ability to obtain a mate through between-individual variation in times of  
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31 394 territory establishment and courtship display (i.e., by sexual selection)[104], while female  
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33 395 reproductive success is predominantly determined by fecundity selection (i.e., her ability to lay eggs  
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35 396 at the right time of year). The circadian hormone melatonin plays a role in the seasonal expression of  
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37 397 song in male song birds, which is an important signal in sexual selection (see section on dawn song  
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39 398 above). Like in other vertebrates, photoperiod, i.e. the length of the daily light phase determines the  
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41 399 duration of nocturnal melatonin release in birds, thus providing an internal signal for the time of  
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43 400 year [30]. Melatonin receptors are present in various brain nuclei that are involved in song  
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45 401 production [107–109] and melatonin contributes to regulating the photoperiodically-induced timing  
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47 402 of song [110]. Thus individual variation in the melatonin signal or its transduction at the receptor  
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49 403 level could influence the time of year when males begin to display song at the beginning of the  
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51 404 reproductive season. Direct tests of this pathway in natural populations are still lacking.  
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405 What has been attempted, however, is to link circadian clock genes with broad-scale population-  
 406 level variation in breeding times across latitudes. In some species including blue tits, there is  
 407 evidence for latitudinal clines in *Clock* gene polymorphisms [111,112]. Furthermore, the *Clock*  
 408 genotype shows a weak relationship with individual variation in breeding time in blue tits, though  
 409 only in females (and not in males, [113]). In barn swallows (*Hirundo rustica*), *Clock* gene diversity as  
 410 well as clock gene methylation is linked with individual variation in breeding time [48,114].  
 411 Understanding whether clock genes and/or their methylation causally underlie these relationships  
 412 that can be sex-dependent, and are present in some species but not others [115], clearly requires  
 413 further work. Furthermore, investigations of whether these core clock genes are amenable to sexual  
 414 selection are also still lacking (see also [116]).

415 Migratory species that spend the winter away from their breeding habitats need to return to their  
 416 breeding grounds before the reproductive season begins. While there undoubtedly exists fecundity  
 417 selection on arrival times (simply because birds first need to arrive to be able to breed), sexual  
 418 selection is also assumed to play a major role [117,118]. Sexual selection should promote earlier  
 419 arrival times of males compared to females, through 'rank advantage' (male-male competition over  
 420 high-quality territories selects for the earliest arriving males) and/or 'mate opportunity' (early  
 421 arriving polygynous males benefit from reduced sperm competition and increased mating  
 422 opportunities [117,119–121]). Timing of migration has, at least in some species, been linked with  
 423 polymorphisms both in *Clock* and in its paralog *Npas2* [122–124][125].

424 At the end of the breeding season, many seasonally breeding species replace their colourful  
 425 breeding plumage with duller feathers (post-breeding or pre-basic moult). Individuals that re-  
 426 achieve their breeding plumage through the subsequent prenuptial/alternate moult earlier in the  
 427 breeding season should also be favoured by sexual selection [126], because brighter individuals are  
 428 more successful in competitive interactions and mate choice, thereby benefitting from increased  
 429 reproductive success (reviewed in: [127]). The best evidence thus far for sexual selection on the

430 timing of moult comes from studies on fairy wren species (*Malurus* spp.) [126]. Males of most fairy  
 431 wrens display delayed plumage maturation, i.e., they moult into brighter plumage as they age. In  
 432 superb fairy wrens (*Malurus cyaneus*) the earlier a male moults into breeding plumage, the more  
 433 likely he is to increase his fitness by extra pair paternity [128–130]. Indeed, a multi-year study found  
 434 strong evidence for directional selection in promoting early moult in males [131].

435 Another excellent example for the importance of timing in sexual selection is the behavioural  
 436 modification of the conspicuous male plumage in rock ptarmigan (*Lagopus muta*; [132]). While  
 437 females moult into their cryptic breeding plumage around the time of snow melt, the males remain  
 438 brilliantly white for at least 3 weeks longer. Their cryptic winter plumage thus not only serves as an  
 439 attraction display during the mating season but also makes males highly vulnerable to predation  
 440 from hawks, particularly gyrfalcons (*Falco rusticolus*). The dazzling male white plumage comes at a  
 441 high cost and may thus form an "honest signal" to available females and in male-male competition.  
 442 As soon as the female begins egg incubation and can no longer be fertilized, the male starts soiling  
 443 his plumage through mud- and dustbaths thereby becoming cryptic before the 2-3 week long moult  
 444 into summer plumage is achieved. Interestingly, polygamous and bachelor males remain white for  
 445 longer, thus increasing their chances of extra-pair copulations. Should the female lose her clutch and  
 446 become receptive again, the male immediately cleans his plumage to become conspicuous again  
 447 [132]. This precise timing of male conspicuousness in relation to female fertility indicates that the  
 448 delayed male spring moult as well as the timing of dirtying is under strong sexual selection.

449 Taken together, many lines of evidence suggest that sexual selection may shape the timing of avian  
 450 seasonal processes like reproductive behaviour, migration and moult that are based on biological  
 451 clocks. Complexity in understanding both selection pressures on and molecular mechanisms of  
 452 annual timing is added by the fact that subsequent seasonal events can depend on each other and  
 453 possibly constrain the action of sexual selection on individual seasonal components. For example, a  
 454 change in the timing of one seasonal event like migration can have significant carry-over effects on

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3 455 subsequent events including reproduction and moult [133]. Such carry-over effects could result from  
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5 456 trade-offs (individuals investing into reproduction may not be able to invest into moult at the same  
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7 457 time) and/or of changes to aspects of the biological clock.  
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#### 11 459 **Timing as a sexually selected trait in mammals**

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14 460 Whether sexual selection exists among mammals on timing during the breeding season, either on  
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16 461 daily or annual processes is presently unclear. This, we propose, is at least in part due to the very  
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18 462 few studies of biological timing and consequences for reproductive success in free-living mammals  
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20 463 that are detailed enough to address this question (and the few existing ones were conducted  
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22 464 primarily on squirrels (*Sciuridae* [116–120])). This may arise from the fact that field studies of daily  
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24 465 and annual patterns of behaviour are logistically challenging, especially when a fine resolution of  
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26 466 daily or seasonal patterns of individuals of both sexes along with estimates of individual  
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28 467 reproductive success is required (though research on ecology and natural selection has clearly been  
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30 468 done (see for example [134,135,137–143])). Some of these hurdles can be overcome by employing  
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32 469 small biologging devices which today allow collection of long-term and precise biological data from  
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34 470 even quite small free-living mammals [144,145]. In addition, there are the associated difficulties in  
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36 471 determining paternity of these same animals. Although there are published studies of paternity in  
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38 472 free-living mammals (e.g., [146–150]), we are not aware of any studies of free-living mammals that  
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40 473 detail both biological timing of males and females and individual reproductive fitness. The question  
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42 474 remains as to whether mating displays by male mammals at specific times of day or earlier or later in  
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44 475 a season are reliable indicators of quality or if females preferentially choose mates based upon their  
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46 476 circadian or circannual proclivities. In the field, selection of mates is driven in part by availability  
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48 477 [151,152] as well as by pre- or post-copulatory choice related to perceived mate quality [153,154].  
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50 478 Thus, the potential for sexual selection exists, but requires further studies.  
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3 479 Despite a dearth of empirical evidence, we contend that for some species it is probable that daily or  
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5 480 annual timing of mating is a sexually selected character trait in mammals. Below we discuss the  
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7 481 potential for sexual selection on circadian and circannual timing in ground squirrels (*Sciuridae*),  
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9 482 species that exhibit a relatively short gestational period and strong endogenously driven circannual  
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11 483 rhythm of hibernation and reproduction [155] [156,157] [158].  
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14 484 Do female ground squirrels prefer early emerging males?  
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16 485 Seasonal timing of reproduction may be most critical to the arctic ground squirrel (*Spermophilus*  
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18 486 *parryi*) owing to the environmental conditions of their high latitude distribution. Overwinter they  
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20 487 are exposed to extremely low temperatures during hibernation, with hibernacula temperatures to  
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22 488 minima of -25°C. The brevity of the arctic summer necessitates mating to occur in the early spring  
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24 489 when air temperatures are well below freezing, snow blankets the tundra and green-up is weeks  
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26 490 away [159]. For males, high thermogenic costs of terminating hibernation at low ambient  
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28 491 temperatures [160–162] and lack of available forage on the surface in spring [163] are off-set by  
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30 492 exogenous energy stores in the form of food cached in the previous summer and fall [136]. In spring,  
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32 493 male arctic ground squirrels draw from these food caches to fuel their ~30 day pre-emergent  
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34 494 euthermic interval needed for reproductive development [165] and to recoup lost body mass  
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36 495 overwinter [159]. Because arctic ground squirrels are solitary hibernators, males are presented with  
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38 496 the challenge of prognosticating when to end hibernation and initiate reproductive development  
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40 497 relative to timing of the end of hibernation of females. Ending heterothermy and initiating  
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42 498 reproductive development too early in the season risks starvation after the food cache is consumed  
43  
44 499 and before females emerge to the surface. Because androgens inhibit expression of torpor  
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46 500 [166,167], re-entering hibernation once reproductive development has begun is not possible.  
47  
48 501 Alternatively, ending heterothermy too late ensures that females are already impregnated during  
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50 502 the approximately 10 day long mating season [168]. On average, females are impregnated within  
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52 503 about 2 days of ending heterothermy [169]; thus, reproductive success of male arctic ground  
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504 squirrels depends upon ending heterothermy and initiating reproductive development *at the right*  
505 *time* relative to when females emerge from hibernation.

506 Although there is considerable variation in timing of emergence of reproductively competent males  
507 between populations [169], within a population emergence timing of reproductive males is highly  
508 synchronized and occurs within about 12 days with >70% of reproductive males on the surface  
509 before emergence of the first female [168]. This occurs despite the fact that animals are in solitary  
510 hibernation with no access to environmental cues for up to 270 days [170][171]. Males that  
511 successfully accumulate and defend a cache prior to hibernation can end heterothermy with  
512 sufficient time to increase body mass and become reproductively competent to compete for mating  
513 opportunities with other males. It is clear that timing is critical to reproductive success of arctic  
514 ground squirrels and it is possible that females select males based on their seasonal emergence  
515 times. However, many open questions remain, for example which cues females use to distinguish  
516 among males with different emergence times since females emerge much later.

517 Within the daily cycle, is there evidence that females exhibit a preference for males at a specific time  
518 of day? Upon emergence from hibernation, both male and female arctic ground squirrels initiate  
519 robust diurnal rhythms in body temperature and activity [136] and are active during the day [172].

520 Observation and quantification of courtship, mating and female choice in field studies have not been  
521 done, quite likely because copulations in free-living ground squirrels are rarely witnessed and are  
522 thought to most commonly occur underground [172]. The ground squirrel mating system is a  
523 scramble competition characterized by intense agonistic interaction among males [168,173]; females  
524 rarely refuse courtship advances by males but reproductive attempts are known to be interrupted by  
525 other competing males [150]. For ground squirrels, it appears that the challenge for males is finding  
526 receptive females and subsequent defence of that female from intruding male for sufficient  
527 duration. Whether female mate choice occurs is not yet clear. Male European ground squirrels  
528 (*Spermophilus citellus*) are known to initiate activity earlier in the day ([174], Fig. 4) than do females,

529 a characteristic that may serve to provide priority access to females ahead of later sleeping  
 530 counterparts. Future work in European ground squirrels may be fruitful to address possibilities of  
 531 sexual selection on daily timing.

532 Taken together, in some mammalian species it seems probable that circadian timing, circannual  
 533 timing or both may be used as a sexually selected trait, but definitive proof is lacking. It is possible  
 534 that the ideal study system for addressing mammalian sexual selection for circadian or circannual  
 535 traits has yet to be found, but it also seems likely that vast existing datasets on sexual selection have  
 536 not been fully exploited to address these issues. Another rewarding research area to explore further  
 537 is that of potential indirect effects of sexual selection on seasonal timing in mammals. For instance,  
 538 it has been argued that sexual selection has favoured sexual dimorphism in body size that can be  
 539 rather pronounced in some mammal species (e.g., [175]). Size dimorphism in turn has allometric  
 540 consequences, generating sex differences in morphology, physiology and life history including in  
 541 metabolic rate and reproductive costs [175]. Hence, sexual size divergence can affect habitat use,  
 542 and time and energy budgets (e.g. in marine mammals, [176,177]), possibly leading to differences in  
 543 seasonal rhythms between males and females. Energy budgets and requirements can also affect  
 544 daily foraging rhythms, the temporal niche utilized (day-, night- or crepuscular activity) and thus  
 545 circadian organisation as well (reviewed in [44]). Indirect effects of sexual selection can therefore  
 546 permeate an array of organismal traits, including seasonal and daily timing. However, the causes and  
 547 mechanisms underlying sex-differences in timing that are generated by such indirect effects of  
 548 sexual selection still need to be clarified in natural populations (but see [44]).

549

## 550 **Conclusions and future perspective**

551 Sexual selection is a well-studied area in evolutionary biology resulting in an ongoing flow of  
 552 scientific papers mainly discussing the ornaments and behaviours involved. The *timing* of displaying

behaviour, however, has received much less attention as a sexually selected trait in itself. In this review we focused on two aspects of timing that may play a role as a sexually selected trait: daily timing and seasonal timing. Various cases have been described where both aspects of timing may be seen as sexually selected traits. The underlying neurobiological mechanisms of annual timing of physiology of moult and reproduction show that circadian clock genes play an essential role in both daily and annual timing. This opens the interesting possibility that daily timing of displaying behaviour may actually form a signal for the seasonal timing of the signalling animal. Future studies could therefore specifically test whether sexual selection may act upon the shared genes in seasonal and daily timing.

With the advent of technologies like biologging and tracking devices we think that it is possible to address many of the open questions that we have outlined throughout this review in field populations – in birds, and especially also in mammals [142,145,178]. This will require long-term detailed behavioural studies to address how timing of displaying behaviour varies among individuals and how this variation relates to annual timing and reproductive success. Again, we note that such studies should be conducted on both sexes, as our brief review showed the existing studies to be biased towards males (for a similar bias in circadian studies of laboratory rodents see [179]). On the other hand, many existing studies on sexual selection may have never considered the importance of timing of displaying behaviour as a trait in itself. It is possible that in addition to the importance of, say, antler size, feather colouration, or complexity of bird song it is also important *when* these traits are being used. This implies that studies on sexual selection may already have recorded timing of displaying behaviour, but never considered it as an important feature. Many data to test some of our hypotheses might therefore already exist. Moreover, in addition to studying the timing of display as an individual trait underlying sexual selection, we need to begin integrating issues of timing with trait quality. The quality of a trait undoubtedly matters in both intra- and intersexual selection and there may be important, but complex interactions with the timing of display (Fig. 1). Importantly, molecular advances now allow us to address questions regarding the specific genes and clock



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3 579 components that may be targeted by sexual selection [180]. Indeed, our review of select examples  
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5 580 illustrates that there have been several attempts in recent years to take advantage of established  
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7 581 molecular pathways in chronobiology to determine the genes that may underlie both daily and  
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9 582 seasonal phenotypes. This field is ripe for detailed conceptual and empirical work on the timing of  
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11 583 trait expression and the actions of sexual selection in birds, mammals and other taxa.  
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**Figure captions:**

**Figure 1:** Hypothetical surface profile representation of the timing of a trait and its interaction with the quality of its expression (e.g., size, colour, complexity). Examples for specific traits could be bird song, or ornaments in birds and mammals. Sexual selection would favour an early expression of this trait while fecundity/viability selection may act against an early display. Likewise, sexual selection would promote a high quality of trait expression while fecundity/viability selection would act against the expression of the highest quality traits. Consequently, only individuals of the highest quality would be able to sustain the costs of displaying this trait early and at high quality, but would gain maximal reproductive success. Specifics of surface profile depend on parameterisation of model, and this representation serves mainly illustrative and not quantitative purposes. For additional explanations please see text.

**Figure 2:** Daily and annual timing share neurobiological and molecular pathways. In birds and mammals the annual timing mechanism uses input from the circadian (daily) timing mechanism at the neurobiological and at the molecular level. In birds (A), light regulates the circadian system through photoreceptors in the pineal gland and various opsin-expressing brain areas, with the eyes playing a species-specific role in circadian organisation. The avian pineal gland produces melatonin and contains a self-sustained circadian oscillator which, together with the suprachiasmatic nucleus (SCN), regulates daily timing in physiology and behaviour. In mammals (B), light input from the retina stimulates the SCN, which regulates daily timing in behaviour, physiology, and melatonin production in the pineal gland. Melatonin receptors in the pars tuberalis of the pituitary (PT) regulate annual timing by thyroid-stimulating hormone (TSH) signalling to the tanycytes in the 3rd ventricle (3V) wall, which in turn regulate thyroid hormone and gonadotropin-releasing hormone signalling regulating gonadotropin secretion by the PT and subsequent annual timing of reproduction. Contrastingly, in birds (A), melanopsin-positive cerebrospinal fluid-contacting neurons in the 3V wall can directly signal photoperiodic information to the PT-tanycyte pathway regulating annual timing of

reproduction. At the molecular level, the core vertebrate circadian oscillator (C) consists of the Bmal1::Clock transcription factor inducing Per and Cry genes which, after dimerization, repress their own promoter activation by the Bmal1::Clock dimer. This oscillatory feedback mechanism causes rhythmic induction of Bmal1 which, after dimerising with Clock, produces circadian regulation of output genes like Tef, Hlf and other clock controlled genes regulating daily rhythms in cellular physiology and metabolism. Synaptic light input signalling to the SCN causes Per induction and entrainment to the external light-dark cycle. In mammals, a similar circadian feedback network resides in the PT (D), but here melatonin induces Cry, while Bmal1::Clock induced Tef and Hlf enhance Bmal1::Clock induction of Eya3. Under long winter nights, the induction of Eya3 is fully blocked by melatonin still present in the morning. When morning melatonin is absent during long summer days, Eya3 will cause TSH release, leading to tanycyte thyroid hormone production and, in long day breeders, to subsequent gonadotropin production by the pituitary leading to seasonal gonadal development. See [www.genecards.org](http://www.genecards.org) for full names of abbreviated genes.

**Figure 3:** Onset of daily activity influences reproductive success. (a) Treatment of wild great tit males with a melatonin implant delayed their activity onset (data represent individual averages from 2-19 days of recording), (b) and melatonin-treated males also suffered a greater cuckoldry risk (higher proportion of extra-pair young in their nest). Data points represent mean values for individuals, and vertical lines indicate the mean  $\pm$  SEM for each treatment group. Data from [78].

**Figure 4:** Timing of daily activity onset (x-axis) in adult European ground squirrels at different seasonal stages (y-axis). Males: filled symbols and solid lines, females: open symbols and broken line. During the pre-mating and mating phases males are active at earlier times than females, while the opposite pattern occurs during lactation and pre-hibernation. Redrawn after data from Everts et al. [174]

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Figure 1

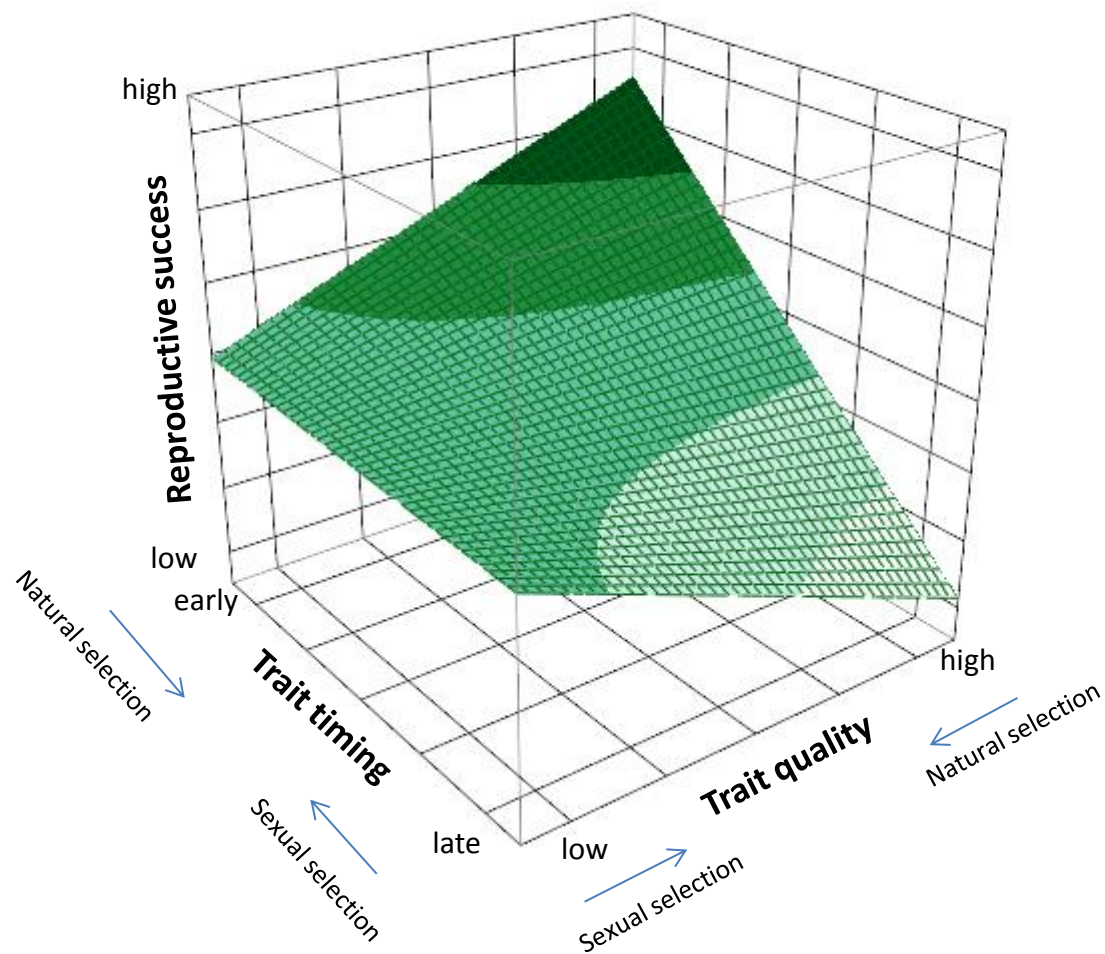
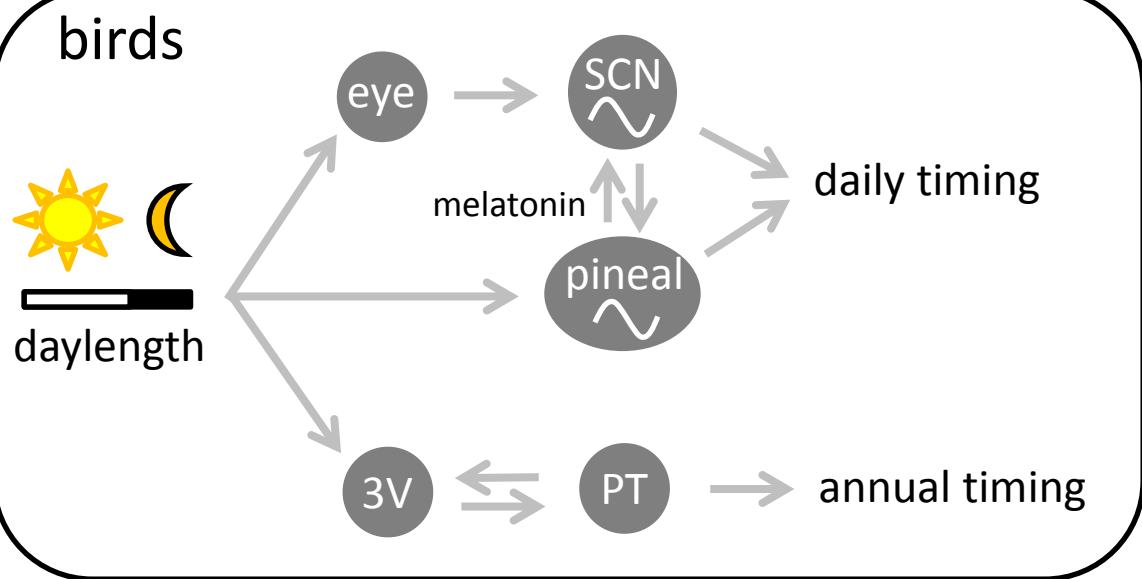
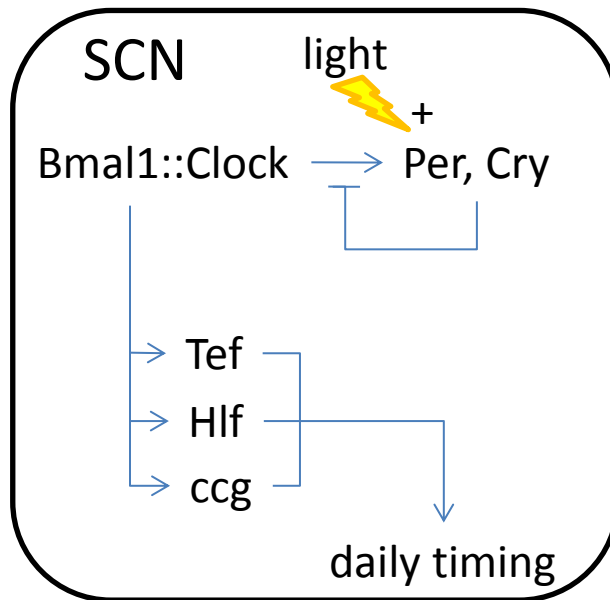


Figure 2

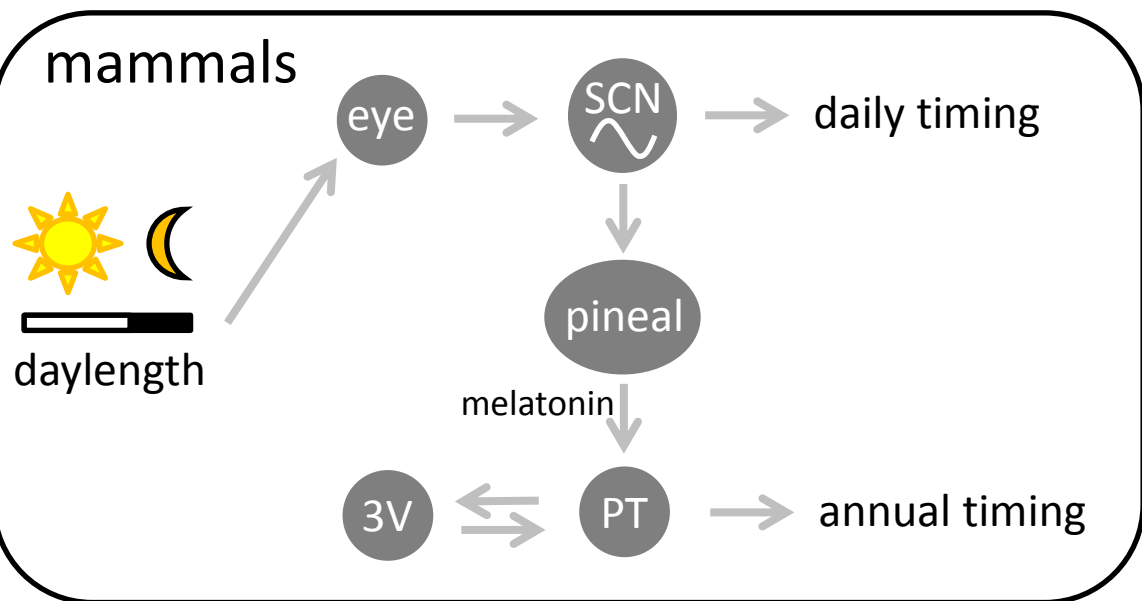
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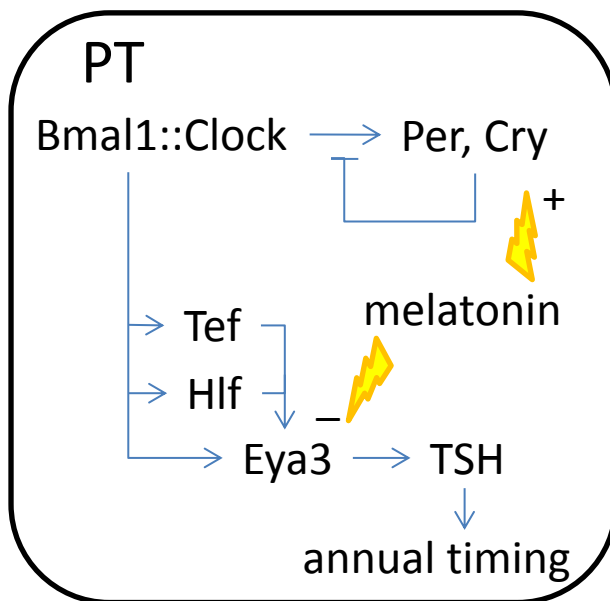


Figure 3

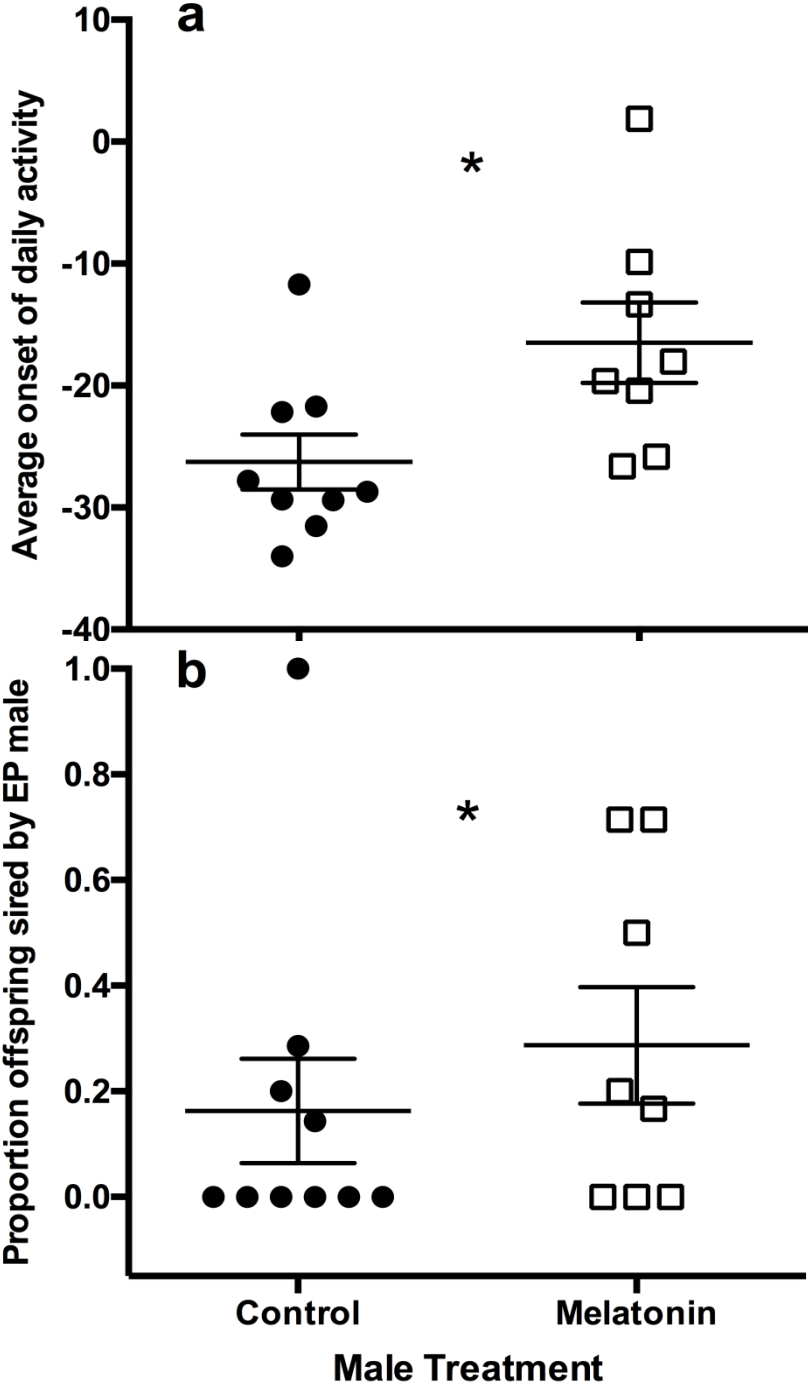


Figure 4

Progress of reproductive season

Pre-mating/mating

Mating/gestation

Lactation

Pre-hibernation

7:20 7:30 7:40 7:50 8:00 8:10 8:20 8:30 8:40 8:50 9:00

Daily activity onset (MET)

